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## Human demography changes in Morocco and environmental imprint during the Holocene

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(Article begins on next page)

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## 3 **Human demography changes in Morocco and environmental imprint** 4 **during the Holocene**

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27 cover

### 28 ***Abstract***

29 The aim of this work is to reconstruct the periods of growth and decline of human  
30 populations in Morocco and their potential impacts on the landscape over the last 10,000 years.  
31 In order to estimate trends in human population size between 10,000 and 3,000 years ago we  
32 used a Summed Probability Distribution (SPD) of radiocarbon dates from a wide range of  
33 archaeological sites throughout Morocco. Landscape changes were identified and quantified  
34 from a data set of fossil pollen records. Different anthropogenic pollen markers, as well as  
35 natural vegetation groups and taxonomic richness were used to analyze the relationship  
36 between long-term trends in human population expansion or regression and type of impact on  
37 the landscape.

38 Sub-regions of Morocco have different topographies and climates, which have either  
39 favored or prevented the establishment and/or spread of human populations. In order to  
40 identify areas most significantly impacted by humans and the timing of such impacts we have  
41 reconstructed and compared the same past anthropogenic and landscape proxies along with  
42 population trends within the lowlands and the mountainous areas. The lowlands were more  
43 strongly impacted earlier in the Holocene than the mountainous areas. Anthropogenic markers  
44 indicate that farming expanded in the lowlands during the first major expansion of human  
45 populations between ca. 7200 and 6700 calibrated years BP at the start of the Neolithic period.  
46 In the Atlas and Rif Mountains anthropogenic impact is not clearly detectable in any of these  
47 areas before 4000 cal. BP.

## 48 **Introduction**

49 Humans have been present in the northwest corner of Africa throughout the Quaternary.  
50 For example, fossil remains of *Homo sapiens* more than 300,000 years old were recently  
51 discovered in Jebel Irhoud, near the town of Safi in Morocco (Hublin et al. 2017). This time span,  
52 which encompasses the latter part of the Palaeolithic period, witnessed three climatic cycles  
53 with marked interglacials that were similar to the Holocene, and long glacial periods (e.g. Hays  
54 et al. 1976). . During the most recent glacial period, around 20,000 years BP, glaciers developed  
55 even at low latitudes, such as within the Mediterranean (Hughes et al. 2006) including North  
56 Africa at elevations as low as 2000 m a.s.l. (Hughes et al. 2011, Hughes et al., 2018). As a  
57 consequence, plant and animal species were naturally constrained, which reduced their range  
58 substantially and allowed them to persist only in refugial areas (e.g. Hewitt, 2000). Likewise,  
59 humans would have adapted their population size and habitats locations in response to past  
60 climate fluctuations (Roberts et al. 2018; van de Loosdrecht et al., 2018).

61 The recolonisation of new suitable habitats by humans after the last glacial period from  
62 scattered populations was probably neither synchronous throughout the Mediterranean nor  
63 continuous and homogeneous during the Holocene warm period (Hajar et al. 2010; Mercuri and  
64 Sadori 2012). This may explain the asynchronous dating of the beginning and end of the  
65 Neolithic in the Mediterranean (Morales et al. 2013; Linstädter et al. 2018). In terms of impact  
66 on the landscape, as soon as human populations began to settle and/or to spread in the  
67 Mediterranean basin they left clear imprints of their activities (cultivation, fire, domestication,  
68 clearing, use of tools etc.) directly in the areas they occupied and indirectly in the fossil records  
69 preserved in wetlands sediment archives and lakes. Most Holocene fossil records tend to show  
70 that there were natural changes during the first thousand years of the Holocene when climate  
71 mainly forced ecosystem changes, which was followed by complex interactions with increasing  
72 human interference. Some authors have proposed that climate was the main driver of  
73 synchronous ecosystem changes in the Mediterranean during the entire Holocene and that  
74 landscape changes cannot be attributed to human activity alone (Jalut et al. 2009). Other  
75 scholars have argued that there is an interplay between climate, humans and Mediterranean  
76 ecosystems, which becomes complex to unravel when aridity increased during and after the  
77 mid-Holocene (Carrión et al. 2010; Mercuri 2008; Sadori et al. 2011).

78 In Morocco, the earliest Holocene human use of plant resources was detected in the semi-  
79 arid lowlands of the Northeast Moroccan hinterland. Charcoal samples from rock shelters  
80 (Grösdorf and Eiwanger, 1999) and Epipalaeolithic open air sites (Ibouhouten et al., 2010,  
81 Linstädter et al., 2012; Mikdad et al., 2000) provide <sup>14</sup>C ages between 11,700 and 7,800 years  
82 cal. BP. In the Middle Atlas Mountains, there are indications of early Holocene occupation  
83 during the Epipalaeolithic with chronological evidence dating to around 8,400 cal BP from  
84 Ouberid cave (Mikdad et al. 2012). However, the ecological impact of Epipalaeolithic hunter-  
85 gatherers on the Early Holocene landscape was minor, therefore this early occupation is not  
86 clearly reflected in secondary environmental archives. The first evidence for human impact on  
87 vegetation cover is provided by recent and precise archaeobotanical studies that have dated  
88 the onset of Early Neolithic occupation in northern Morocco, close to the Mediterranean Sea,  
89 between 7700-7200 years cal. BP (Linstädter et al. 2016; Zapata et al. 2013).

90 Indirect evidence from fossil pollen records suggests that human impact has strongly  
91 increased over the last four thousand years in Morocco and became increasingly apparent at  
92 both low and high elevations (Lamb et al. 1991; Cheddadi et al. 2015, Campbell et al. 2017). In  
93 addition to fossil pollen records, model simulations show that during the historic period, forest  
94 cover on usable land may have dropped dramatically from an estimated 98% in 3000 BP to  
95 31.7% in 1850 AD (Kaplan et al. 2009) in relation to the expansion of human population. In  
96 Morocco, cedar forest cover in the Rif mountains decreased by about 75% between 1960 and

97 2010 (Cheddadi et al. 2017).

98 Human activities can be identified in the fossil pollen records through the occurrence and  
99 abundance of those taxa that are considered anthropogenic indicators (Behre 1981; Mercuri et  
100 al. 2011). Changes through time in human population size can also be estimated from the  
101 summed probability distributions (SPD) of archaeological (e.g. anthropogenic) radiocarbon  
102 dates (Crema et al. 2016; Gamble et al. 2004; Palmisiano et al. 2017 and in press; Shennan et al.  
103 2013; Timpson et al. 2014; Weninger et al. 2009; Williams 2012; Zielhofer et al. 2008).

104 In the present study, we estimated the size of human population in Morocco for the time  
105 period between 10,000 and 3000 cal BP and compared population variation during the  
106 Holocene to several anthropogenic pollen indicators as well as to reconstructed natural  
107 vegetation groups and past taxonomic richness derived from an extensive data-set of fossil  
108 pollen records.

109 Morocco has a wide range of topographies with highest elevations ranging from 2500 in  
110 the Rif mountain chain up to more than 4000masl in the High Atlas. There are also large coastal  
111 lands and plains, which are intensively cultivated today. These complex topographic features  
112 have almost certainly constrained the spread and settlement of humans throughout the  
113 Moroccan landscape. The main objectives of this study are threefold (1) to reconstruct overall  
114 human demographic changes in Morocco during the later prehistory (2) to identify different  
115 past human activities in different areas using a set of anthropogenic markers from a dataset of  
116 fossil pollen records and (3) to evaluate the spread of human activities and their impacts both  
117 on the lowlands and mountain landscapes.

## 118 ***Materials and Methods***

### 119 ***Anthropogenic markers, natural vegetation groups and taxonomic richness***

120 The pollen data-set used in the present study includes 22 records from different areas  
121 in Morocco, obtained from both original authors and digitized published work (figure 1A, table  
122 1). There are two sites, Lake Hachlaf and Lake Sidi Ali, where two records were collected in  
123 each lake. We integrated these duplicated records because they encompass different time  
124 periods. The Moroccan pollen records were produced by various analysts over a ca. 40 year  
125 period, between 1976 and 2017 and have been dated relatively accurately by conventional and  
126 AMS radiocarbon dating. Some of the oldest pollen records (Reille, 1976; 1977 and 1979) have  
127 been dated using very few radiocarbon dates. Three pollen records (Marzine in the Rif,  
128 Tessaout and Tizi Inouzane in the High Atlas) for which the published chronologies were based  
129 on just one <sup>14</sup>C date (Reille, 1976; 1977), while one record (Iguerda-Ait-Amama in the Middle  
130 Atlas) has not been dated by any radiometric methods (Reille, 1976). The age/depth models  
131 that we have built for these four pollen records are based on the published original author's  
132 assumptions based on stratigraphic markers and expertise. The time spans proposed by the  
133 original author (Atlantic, Sub-boreal and Sub-Atlantic periods) have been used to build a  
134 quantitative chronology for the four pollen records.

135 Within the dataset, there are five pollen records located at elevations lower than 800m  
136 asl. Two of them encompass the Early Holocene and three others only cover the mid- late  
137 Holocene (after 6500 BP). Thus, in the data-set used in this study, there are more pollen records  
138 that encompass the entire Holocene period in the mountains than in the lowlands. Such bias in  
139 the duration and the spatial distribution of the pollen records in Morocco must be taken into  
140 account when interpreting the occurrence of anthropogenic markers and overall vegetation  
141 changes. All of the pollen records compiled have been archived in a MySQL database, which has  
142 a compatible structure with the European Pollen Database  
143 ([www.europeanpollendatabase.net](http://www.europeanpollendatabase.net)). The Moroccan pollen data will be contributed to the  
144 European Pollen Database (Leydet, 2007-2018).

145 We defined five anthropogenic pollen markers (APMs) from the taxa identified in the  
146 fossil pollen records (table 2). These APMs are based on earlier published research and are  
147 considered indicative of human activities (Behre 1981; Mercuri 2008; Mercuri et al. 2011;  
148 2013a; 2013b; Sadori et al. 2011). The reconstructed APMs include:

- 149 - Anthropogenic pollen index (API)
- 150 - Regional pastoral indicators (RPI)
- 151 - Anthropogenic nitrophilous herbs (ANH)
- 152 - Cultures and crops (CC)
- 153 - *Olea-Juglans-Castanea-Vitis* (OJCV)

154 We selected these five APMs to allow comparisons with a selection of similar studies  
155 based on six other regions spanning the Mediterranean and a Mediterranean-wide synthesis of  
156 Holocene population and landscape change (see Bevan et al., in press, Roberts et al., in press).  
157 In Morocco, these APMs were reconstructed for three separate regions: the Rif Mountains, the  
158 Atlas Mountains and lowland sites (located at an elevation lower than 800m asl). The three sub-  
159 regions were then amalgamated and reconstructions produced, for the entire country as one  
160 overall entity that takes all of the pollen records into account (figure 2). One palynological  
161 difference with these similar studies carried out in other Mediterranean regions is the exclusion  
162 of *Artemisia* from the APMs because it is a natural dominant taxon in Moroccan steppe  
163 landscapes which occurs in the mountainous areas (e.g. Saadi and Bernard, 1991). Thus,  
164 *Artemisia* was not considered an anthropogenic marker in the present study. In addition to the  
165 APMs, we reconstructed the pollen taxonomic richness (figure 3) using rarefaction analysis  
166 (Birks and Line 1992) for the same areas and pollen records as the APMs. Fossil pollen samples  
167 represent a partial representation of the anemophilous plants, due to the differing pollen  
168 productivity of different plants and their dissimilar dispersal capacity. The number of identified  
169 and counted pollen grains is also often, if not always, different from one analyzed sample to  
170 another within the same record. Rarefaction analysis provides an unbiased estimate of the  
171 number of taxa in a fossil sample which allows a comparison of the pollen analyses from  
172 different samples in the same record (Birks and Line 1992). However, one should keep in mind  
173 that the pollen taxonomic richness does not represent a measure of the species diversity, *sensu*  
174 Shannon or Simpson indices, as one pollen taxon may correspond to one or several species and  
175 the pollen percentage in a fossil sample does not correspond to the number of occurrences of  
176 the species in the studied site. Modern human activities often result in negative impact on  
177 species diversity. Pollen taxonomic richness is not a direct indicator of past human  
178 disturbances, but it may help comprehend whether the past human demographic changes had  
179 a negative or positive impact on species diversity.

180 In addition to the APMs and pollen taxonomic richness, we also used clusters of pollen  
181 taxa to identify four natural vegetation groups (figure 4) that represent the main ecosystem  
182 types in Morocco (Quézel and Médail, 2003). These natural vegetation groups are ordered by  
183 increasing elevation (1) evergreen trees and shrubs, (2) deciduous trees, (3) mountain conifers,  
184 and (4) steppe (table 3). This is based on grouping pollen samples into 'vegetation clusters'  
185 according to their taxa assemblages and builds on the cluster analysis approach used by  
186 Woodbridge et al. (2018) and Fyfe et al. (2018).

### 187 **Demographic change over the Holocene**

188 In the past two decades one of the most popular proxies for inferring demographic trends  
189 in the prehistoric period has involved summed probability distributions (SPDs) of  
190 archaeological radiocarbon dates as a result of increasingly sophisticated methods (Rick, 1987;  
191 Shennan and Edinborough, 2007; Bocquet-Appel et al., 2009; Shennan et al., 2013; Timpson et  
192 al., 2014; Balsera et al., 2015; Crema et al., 2016; Bevan et al., 2017; Palmisano et al.; 2017;  
193 Capuzzo et al. 2018). The SPD results from 'counting up' (summed in the manner of a



194 histogram) the calibrated raw radiocarbon years of each organic sample, which are expressed  
195 as probability statements with error ranges. This is based on the assumption that the more  
196 people living in a given region, the more archaeological remains, the more organic materials,  
197 and the more samples can be collected for radiocarbon dating (Rick 1987). Such indicators do  
198 not offer good evidence for absolute numbers of a human population but rather give an idea of  
199 relative intensities of population and proportional change through time. Although SPDs of  
200 radiocarbon dates has been extensively used by archaeologists for modelling population  
201 fluctuations in prehistory, it faces several challenges such as biases in research strategies,  
202 budgets and interests that can undermine a random sample of human activity in every  
203 archaeological phase.

204 Over the past ten years, both the number and the accuracy of radiocarbon dates have  
205 increased in most newly investigated archaeological sites. This is the case in Morocco, where  
206 more than two-thirds of the radiocarbon dates used in the present study were published in the  
207 past decade. In the present study we have estimated human population size in Morocco from  
208 270 uncalibrated radiocarbon dates which have been collected from 83 archaeological sites  
209 (figure 1B) between 10,000 and 3000 cal BP. To our knowledge, the dataset used in this work  
210 represents the largest existing collation of archaeological radiocarbon data for Morocco. This  
211 number of dates collected (n=270) exceeds the suggested minimum threshold of 200-500 dates  
212 to produce a reliable SPD with reduced statistical fluctuation for a time interval of 10,000 years;  
213 specific issues about sample size will be discussed below (Michczyńska and Pazdur, 2004;  
214 Michczyńska et al., 2007; Williams, 2012, 580-581). We are aware of the limitations of our  
215 dataset and the results are a preliminary attempt to reconstruct demographic change given the  
216 spatially restricted archaeological data available in the area.

217 All of the radiocarbon dates are from archaeological contexts, with the majority based on  
218 samples of bone, charcoal and wood. Radiocarbon dates obtained from marine sources, such as  
219 shells have been removed (and are not part of the above total) to avoid the complicated issues  
220 arising from unknown or poorly understood marine reservoir offsets. The probabilities from  
221 each calibrated date have been combined to produce a summed probability distribution (SPD,  
222 figure 5)<sup>1</sup>. The potential bias of oversampling particular site-phases has been reduced by  
223 aggregating multiple uncalibrated radiocarbon dates from the same site that are within 100  
224 years of each other and dividing by the number of dates that fall within this time 'bin' (see  
225 Timpson et al. 2014). Following this process, the probabilities of each bin are summed: in our  
226 case, 270 radiocarbon dates have been aggregated into 207 bins. Following previous works  
227 (Weninger et al. 2015; Williams 2012), which show that normalized calibrated dates emphasize  
228 narrow artificial peaks in SPDs due to steepening portions of the radiocarbon calibration curve,  
229 we opted to use unnormalized dates prior to summation and calibrated via the IntCal13 curve  
230 (Reimer et al. 2013; see former applications of calibrated unnormalized radiocarbon dates in  
231 Bevan et al. 2017; Palmisano et al. 2017; Roberts et al. 2018). A logistic null model representing  
232 expected population increase has been fitted to the observed SPD in order to produce a 95%  
233 confidence envelope (composed of 1,000 random SPDs) and statistically test if the observed  
234 pattern significantly departs from this model (for the general approach see Shennan et al 2013;  
235 Timpson et al 2014; as specifically implemented in Bevan and Crema 2018: modelTest,  
236 'uncalsample'). Deviations above and below the 95% confidence limits of the envelope  
237 respectively indicate periods of population growth and decline greater than expected according  
238 a logistic model of population growth. However, it is important to recognize that a logistic  
239 model cannot strictly be considered as a realistic model for population growth, but rather as  
240 an elementary model useful for quantitatively testing population fluctuations (cf. Turchin

<sup>1</sup> The analysis has been performed in R v. 3.3.3 by using the package *rcarbon* developed by Crema and Bevan (2018).

241 2001). In this case, a logistic model was selected as a more suitable option as opposed to other  
242 possible null-models (e.g. uniform, exponential) given the observed shape of radiocarbon date  
243 SPDs in our study area (see Fig. 5).

244 As proxies for past population estimates from the SPDs of radiocarbon dates can be used  
245 as recently as ~3000 Cal yr BP in Morocco, that is prior to the historical time period when  
246 archaeological chronologies rely more on specific evidence such as datable coins, written  
247 source and fine-ware pottery rather than on radiometric dating.

#### 248 **Chemical elements**

249 A chemical elements analysis was carried out, using portable X-ray fluorescence (XRF)  
250 technique, on a sediment core retrieved in Ait Ichou swamp in the south of the Middle Atlas  
251 (Tabel et al., 2016). XRF analyses allowed the variation of more than 20 chemical elements to  
252 be measured over the past 25,000 years covered by the Ait Ichou core. However, only four  
253 chemical elements were used in this study (figure 6). These elements are iron (Fe), lead (Pb),  
254 zinc (Zn) and copper (Cu). These elements were selected as indicators of human activity and  
255 marked increase of their concentration in the sedimentary record is related to different human  
256 activities in the area.

#### 257 **Results**

258 The compiled fossil pollen data-set (figure 1A) and archaeological radiocarbon dates  
259 (figure 1B) allow us to reconstruct of several anthropogenic markers (figure 2), past plant  
260 taxonomic richness (figure 3), natural composition of past ecosystems (figure 4) as well human  
261 demography changes (figure 5) during the Holocene. The anthropogenic pollen markers allow  
262 us to identify of potential relationships between natural ecosystems and superimposed human  
263 disturbances. A spatial and temporal analysis of these pollen markers may provide information  
264 on the timing of human interference throughout the Holocene and the types of impact. The  
265 proportions of the reconstructed anthropogenic markers correlate with the estimated human  
266 demography, which may provide information about the intensity of human impacts on the  
267 landscape.

268 The archaeo-demographic results (Figure 5) show some significant overall departures  
269 of the SPD of observed data from the envelope of the logistic model ( $p = 0.006$ ), which indicates  
270 that population did not grow logistically from 10,000 to 3000 BP in Morocco. The population  
271 was greater than predicted by the logistic null model in the Middle Holocene between ~7200-  
272 6700 cal. BP and ~6300-6200 cal. BP. In contrast, population was significantly below expected  
273 values in the Early Holocene (~9200-9000 cal. BP, ~8450-8370 cal. BP and ~8200-8000 cal.  
274 BP). Another marked decline in population occurs during 4800-4500 cal. BP. Generally, the  
275 level of population was lower in the Early Holocene and started increasing substantially with  
276 the onset of the Neolithic in the 8<sup>th</sup> millennium cal BP. The duration of these periods of  
277 decreasing and increasing human population differ and varies between ca. one and ca. four  
278 centuries (figure 5).

279 The anthropogenic pollen markers API, ANH and CC show a marked increase (figure 2)  
280 that matches the first significant expansion of human populations between 7180 and 6740 cal  
281 BP (event 4 in figure 5). This first increase in pollen indicators of human activity is recorded  
282 mainly in the lowland sites rather than in the Rif and Atlas Mountains. The arboreal pollen  
283 percentages decrease most significantly within sites located at lower altitude. Human  
284 demographic changes (figure 5) and the three APMs (API, ANH and CC) from the lowland sites  
285 are positively correlated (table 4). Pollen taxonomic richness shows a significant correlation  
286 with SPDs (table 4) with a marked increase between 7180 and 6740 then between 6330 and  
287 6240 when human population also increased (events 4 and 5). This correlation is more

288 significant in sites located in the lowlands than in the Rif and Atlas Mountains (figure 3). Periods  
289 of decreasing human population (events 1, 2, 3 and 6, figure 5) are not marked in the lowlands  
290 or in the mountains. In order to evaluate the impact of human demographic changes on natural  
291 ecosystems we have reconstructed four groups of vegetation (figure 4, table 3), which are well  
292 defined in Morocco (Quézel and Médail, 2003) and pollen grains representing these plant  
293 species have been identified in the fossil records. These vegetation groups include montane  
294 conifers, deciduous trees, evergreen trees and shrubs and steppic plants (figure 4). None of  
295 these groups shows a significant correlation with human demographic changes during the  
296 Holocene (table 4) and none of the human population increases (event 4 and 5) or decreases  
297 (events 1, 2, 3 and 6) clearly reflect changes in any vegetation group.

## 298 **Discussion**

299 The modern challenges facing the Mediterranean region in terms of managing the impacts  
300 of both the climate change and human population growth are intensifying. Human pressures on  
301 Mediterranean biodiversity has steadily increased over the last century and reached a critical  
302 threshold within the last few decades. Understanding of past relationships between human  
303 demography and ecosystem changes is paramount to managing ongoing landscape changes and  
304 requires studies integrating longer time scales than the last few decades.

305 Morocco is within the Mediterranean floristic area, which is considered a hotspot of  
306 biodiversity (Myers et al. 2000) with approximately 22% of endemic vascular plants (Rankou  
307 et al. 2013). Due to the geographical expansion of human population and related activities,  
308 several species have become extinct over the last century and many species are endangered or  
309 in threat of extinction today (IUCN, 2018). Forest cover in Morocco has been decreasing steadily  
310 and substantially over the past century (Kaplan et al. 2009) and all ecosystems, from the  
311 seashore to the highest elevation mountains, have been impacted by expanding human  
312 activities and increasing exploitation of ecosystem resources. For example, cedar forest cover  
313 in the Rif Mountains has decreased by about 75% over the last 50 years, from more than 45k  
314 ha to ca. 10k ha today (Cheddadi et al. 2017). Simultaneously, human population more than  
315 quintupled between 1900 and 2014, from ca. 6 to ca. 34 million inhabitants. In this context,  
316 today more than ever it is important to analyze and understand past impacts of human  
317 demographic change on different ecosystem types. The Neolithic is a very interesting period for  
318 exploring the impact of early human expansions and regressions, on landscapes and the  
319 increasingly complex ways in which such activities are superimposed on climate change  
320 records. This may help to evaluate the ecosystem's capacity for adaptation and resilience to the  
321 combined effects of natural and human induced changes.

322 Evaluation of human demography during the Neolithic can be performed using  
323 radiocarbon dates available from archaeological sites and *ad hoc* statistical tools (Crema et al.  
324 2016; Gamble et al. 2004; Palmisiano et al., 2017; Shennan et al. 2013; Williams 2012).  
325 However, one should be cautious as archaeological sites are often not exhaustively studied and  
326 there may be important differences in the number of dates available at each site. This is clearly  
327 the case for Morocco where the number of <sup>14</sup>C dates used in this study could certainly be  
328 improved with additional archaeological sites and more <sup>14</sup>C dates per site. Other additional  
329 potential biases related to <sup>14</sup>C date measurements and their calibration may also introduce  
330 some errors in estimating human demographic trends using SPDs (Shennan et al. 2013), as well  
331 as the duration of the expansion/regression of human populations (Manning et al. 2014). Used  
332 as a demographic proxy, SPDs may reflect only a local (or regional) expansion of human  
333 population rather than representing a spatially large spread (Shennan et al. 2013).

334 There is a large literature focused on human expansion and related activities in the  
335 Mediterranean basin during the Neolithic (summarized in Shennan, 2018). However, the timing



336 of expansion and, the type and intensity of the impacts are not synchronous and probably not  
337 comparable throughout the Mediterranean region. Today, human population in Morocco is  
338 composed mainly of Berbers (autochthonous population) and Arabs. Genetic analyses of North-  
339 Western African populations reveal that lineages of different Berber groups may date back to  
340 at least the last glacial period and that the omnipresence of a certain mitochondrial DNA motif  
341 suggests a continuous presence of these populations in Morocco over more than 20,000 years  
342 (Rando et al., 1998). All recent genetic studies agree that the spread of human populations in  
343 North Africa originated from the East-West (Bentayebi et al. 2014), rather than originating from  
344 sub-Saharan populations (Desanges, 1981). The genetic contribution of sub-Saharan  
345 populations to the modern North African populations seems to be minor (Bosch et al., 1997;  
346 Brakez et al., 2001). Recent archaeological findings in Northern Morocco indicate the absence  
347 of Saharan influences during the Early Neolithic until 6.0 cal ka BP (Linstädter et al., 2018).  
348 Thus, even if the timing, continuity and degree of expansion of the migrating original  
349 populations is still under scientific debate, the Eastern origin of the modern North African  
350 populations is now genetically proven. Rando et al. (1998) state that the modern dominating  
351 lineages arrived in North Africa, during the Mesolithic and Neolithic in waves while Arredi et  
352 al. (2004) propose that the Neolithic transition in North Africa was accompanied by demic  
353 diffusion (see Cavalli-Sforza et al. 1993). The marked variations in <sup>14</sup>C date SPDs (figure 5) and  
354 the discontinuous occurrences of the fossil anthropogenic markers (figure 2) suggest that  
355 human population in Morocco did not increase steadily during the Holocene, but involved  
356 marked periods of 'booms' and 'busts' that impacted upon the landscape intermittently. These  
357 past demographic variations (figure 5) and discontinuous landscape changes could probably  
358 have resulted from waves of immigrating populations rather than demic diffusion into Morocco  
359 during the Holocene.

360 The SPD data suggest that human demography fluctuated during the Holocene with two  
361 periods of noticeable population increase and four others with noticeable population decrease  
362 (figure 5; table 4). Human population increased substantially with the onset of the Atlantic  
363 Neolithic around 7400/7300 cal BP. In agreement with the SPD data, pollen markers of cultures  
364 and crops and farming increased in sites located at low elevation. The correlation between the  
365 anthropogenic markers and SPD (table 5) suggests that human impact was not only local or  
366 regional, but probably took place over a larger area. However, this positive correlation is based  
367 on only five lowland records, which includes two Holocene archaeological sites (figure 1B, table  
368 1) and three pollen records that encompass the second half of the Holocene (younger than 6500  
369 cal. BP). To confirm that human impact in the lowlands was spatially more extended would  
370 require additional Holocene data from off-site contexts, such as lake sediments at low elevation.  
371 The pollen records available in the Rif and Atlas Mountains are more numerous, well dated and  
372 many of them encompass the entire Holocene (table 1). In these montane records we do not  
373 observe a significant correlation between the APMs and SPDs (table 5) which supports the  
374 interpretation that human imprints were probably restricted to the lowland areas during the  
375 Early Neolithic. Archaeological findings in the Moroccan coastal areas and lowlands confirm the  
376 presence of cultivated landscapes as early as ca. 7000 cal BP (Ballouche and Marival 2003;  
377 Linstädter et al. 2016; López-Sáez and López-Merino, 2008; López-Sáez et al., 2013; Morales et  
378 al. 2013; Zapata et al. 2013). At higher elevations, several palaeoecological studies indicate late  
379 Holocene human impacts on ecosystems in the Atlas and the Rif Mountains (Abel-Schaad et al.  
380 2018; Campbell et al., 2017; Cheddadi et al. 2015; Lamb et al. 1991; Reille 1977; Zielhofer et al.  
381 2017). The low correlation between forest ecosystems (figure 4), which occur mainly in the  
382 mountain areas, and SPDs (table 5) suggest a lower level of human impact at higher elevations.  
383 Inhabitants of the Moroccan mountains may have included populations of hunters-gatherers  
384 rather than farmers, which could have delayed the expansion of cultivation and food production

385 "technologies" (Bosch et al. 1997) and, therefore, may explain the absence or low level of human  
386 imprints during the Early Neolithic in the Rif and Atlas Mountains. Prior to the first period of  
387 significant human expansion (ca. 7400 cal BP) there are high values of OJCV (>10%) that are  
388 dominated by *Olea* pollen percentages, which may be interpreted as related to early  
389 domestication of the olive tree in Morocco. However, these high *Olea* occurrences are recorded  
390 during a time span of significantly lower human population (figure 2). The increase in *Olea*  
391 pollen percentages during the early Holocene in Morocco likely corresponds to the spread of  
392 wild stands (oleaster) under a warmer early Holocene climate (Cheddadi et al. 1998) rather  
393 than to early domestication of the olive tree (see Langgut et al., this volume).

394 Reconstructed pollen taxonomic richness (figure 3) is not well correlated with human  
395 demographic changes either in the lowlands or in the mountainous sites (table 5, figure 3),  
396 which suggests that either human demographic fluctuations had a minor impact on the  
397 structure and composition of the ecosystems or that such ecosystems are highly resilient. This  
398 reflects the characteristics of modern Mediterranean ecosystems, which are considered highly  
399 resilient to human disturbances due to their high ecological diversity (Lavorel, 1999; Pausas et  
400 al. 2008).

401 After the first major increase in human population (7180-6740 cal BP) we observe a  
402 quasi-steady decreasing trend, which reached a noticeable SPD minimum between ca. 4820 and  
403 ca. 4530 cal BP (figure 5). The anthropogenic markers (API, ANH and CC) also decreased in the  
404 lowlands and remained low in the Rif and Atlas Mountains (figure 2) during this time, which is  
405 coherent with the reconstructed decreasing trend in human population. Within the Rif  
406 Mountain archaeological sites cereals and anthropogenic herbs decreased between 6700 and  
407 6000 cal BP, indicating reduced grazing and cultivation activities (Linstädter et al. 2016). The  
408 SPD data indicate that human population remained low until 4000 cal BP, which probably  
409 marks the end of the Neolithic in Morocco.

410 Unlike other parts of the Mediterranean, the metal ages (Bronze, Copper, Iron) are not  
411 well dated in Morocco. X-Ray fluorescence measurements of the fossil record in the southern  
412 part of the Middle Atlas (Tabel et al. 2016) show that iron (Fe), lead (Pb), copper (Cu) and zinc  
413 (Zn) started to increase significantly after 4000 cal BP (figure 6) which seems to be earlier than  
414 in other parts of the Mediterranean (Van Der Plicht et al. 2009), and coherent with earlier  
415 archaeological studies in Morocco (Daugas et al. 1998; Ballouche and Marinval 2003). Chemical  
416 elements (Fe, Cu, Zn and Pb) are often associated with human activities during the metal ages  
417 (i.e. the Bronze and Iron Ages) probably mark the beginning of an "industrial" period dedicated  
418 to their extraction. The SPD data cover the period between 10000 and 3000 cal BP, which does  
419 not allow exploration of human demographic changes during the Iron age. In the northern part  
420 of the Middle Atlas, and increase in lead concentration (Pb) in a fossil record (Nour El Bait et al.  
421 2014) started around 2000 cal BP, which corresponds to the beginning of the Roman presence  
422 in Morocco. In the Rif Mountains, the geochemical content of several records show similar  
423 changes to those of the Middle Atlas after 2000 cal BP and are clearly related to Roman  
424 industrial activities, which started to impact upon mountain ecosystems, such as through the  
425 degradation of the Atlas cedar forests (Cheddadi et al. 2015). The impact of Roman activities in  
426 Morocco seems to have been more critical for forest ecosystems with a decrease in arboreal  
427 pollen percentages (figure 2), particularly those of the deciduous and evergreen trees (figure  
428 4).

429 It is interesting to note that taxonomic diversity, as detected by pollen records, (figure 3)  
430 was not altered during the Neolithic nor the Bronze/Iron Ages and not even during the Roman  
431 period. Today, areas rich in endemic species are threatened by the wide range of human  
432 activities particularly in areas identified as biodiversity hotspots such as the Mediterranean  
433 (e.g. Cincotta et al. 2000). Pollen taxonomic richness in Morocco actually shows a relatively

434 steady increase throughout the Holocene and increases more over so throughout the last 3000  
435 years during the metal ages. Elsewhere, several paleoecological studies have also shown that  
436 the last thousand years of the Holocene are marked by an increase in pollen taxa richness (e.g.  
437 Birks and Line 1992; Lotter 1998), which is paradoxical with the modern negative impacts of  
438 human activities on ecosystems and their species richness, but perhaps consistent with the  
439 well-known (but debated) intermediate-disturbance hypothesis (e.g. Fox, 2013). Unlike during  
440 the modern industrial era, human activities during earlier periods of the Holocene, which  
441 mainly involved livestock grazing and cultivation, were excellent means for the dispersal of  
442 seeds, propagation of domesticated plants and the dispersal of ruderal plants that are often  
443 subservient to crops.

444 Our study suggests that there are major differences between past and modern human  
445 activities, such as modern artificial reduction of species ranges through the industrial  
446 exploitation of forest resources (e.g. Pearson and Dawson 2003), mono-specific plantations  
447 over large areas (Brockerhoff et al. 2008), the introduction of invasive and alien plant species  
448 which strongly and negatively disturb ecosystem composition (Thuiller et al. 2005), the  
449 widespread use of herbicides and pesticides, and the abruptness of ongoing climate change  
450 (<http://www.ipcc.ch/>) which restricts species ranges. Modern human activities are causing  
451 rapid, novel, and substantial changes to Earth's ecosystems (Vitousek et al. 1997; Nolan et al.,  
452 2018) that we have not observed in our Holocene records in Morocco.

## 453 **Conclusions**

454 The last 10,000 years represent an informative time span encompassing the spectrum of  
455 natural to anthropogenic forcing, which includes a period of natural climatic changes, with  
456 negligible human impact in the early Holocene, followed by a period of interplay between  
457 natural and anthropogenic impacts with the expansion of human populations.

458 The archaeological and environmental data used in this study indicate that prior to 7400  
459 cal BP human populations had a limited impact on the lowland landscape and mountain  
460 ecosystems. The earliest significant expansion of human population in Morocco during the  
461 Holocene took place around 7000 cal BP and it is marked in the fossil pollen record by an  
462 increase in farming indicators, particularly crop pollen markers. This time span is a few  
463 hundred years later than the beginning of the Neolithic period in Morocco and ends around  
464 4000 cal BP when iron, copper and zinc content started to increase in sedimentary records.  
465 Geochemical elements were extracted to make metal tools, which marks the end of the Neolithic  
466 period and probably the beginning of a prehistoric metallurgical industry era. We observe that  
467 several anthropogenic indicators increase when human population increases. Likewise, natural  
468 ecosystem changes, including forest species, are negatively or positively impacted by an  
469 increase or a decrease in human population size during the Holocene, respectively.

470 The correlations we have performed between <sup>14</sup>C date SPDs, as a proxy for population  
471 change, and the fossil pollen data suggest that:

472 (1) early expansion of human populations around 7000 cal BP took place mainly in the  
473 lowlands and if there was a spread towards the mountain areas then it was either minor or the  
474 spreading populations had a negligible impact on natural ecosystems. However, early Holocene  
475 anthropogenic evidence is derived from very few lowland sites. To confirm whether there was  
476 a more extensive vegetation change additional data from archaeological off-site contexts, such  
477 as lake sediments, are still needed.

478 (2) the principal human activity detected in the lowland records involved grazing and  
479 farming until ca. 4000 cal BP.

480 (3) plant domestication seems not to have taken place before the early expansion of  
481 human populations in Morocco, which is recorded during the Neolithic around 7000 cal BP.

482           The conclusions drawn in the present study have potential to be clarified through  
483 integration of additional archaeological sites with more radiocarbon dates and new fossil pollen  
484 records from lower elevations areas.

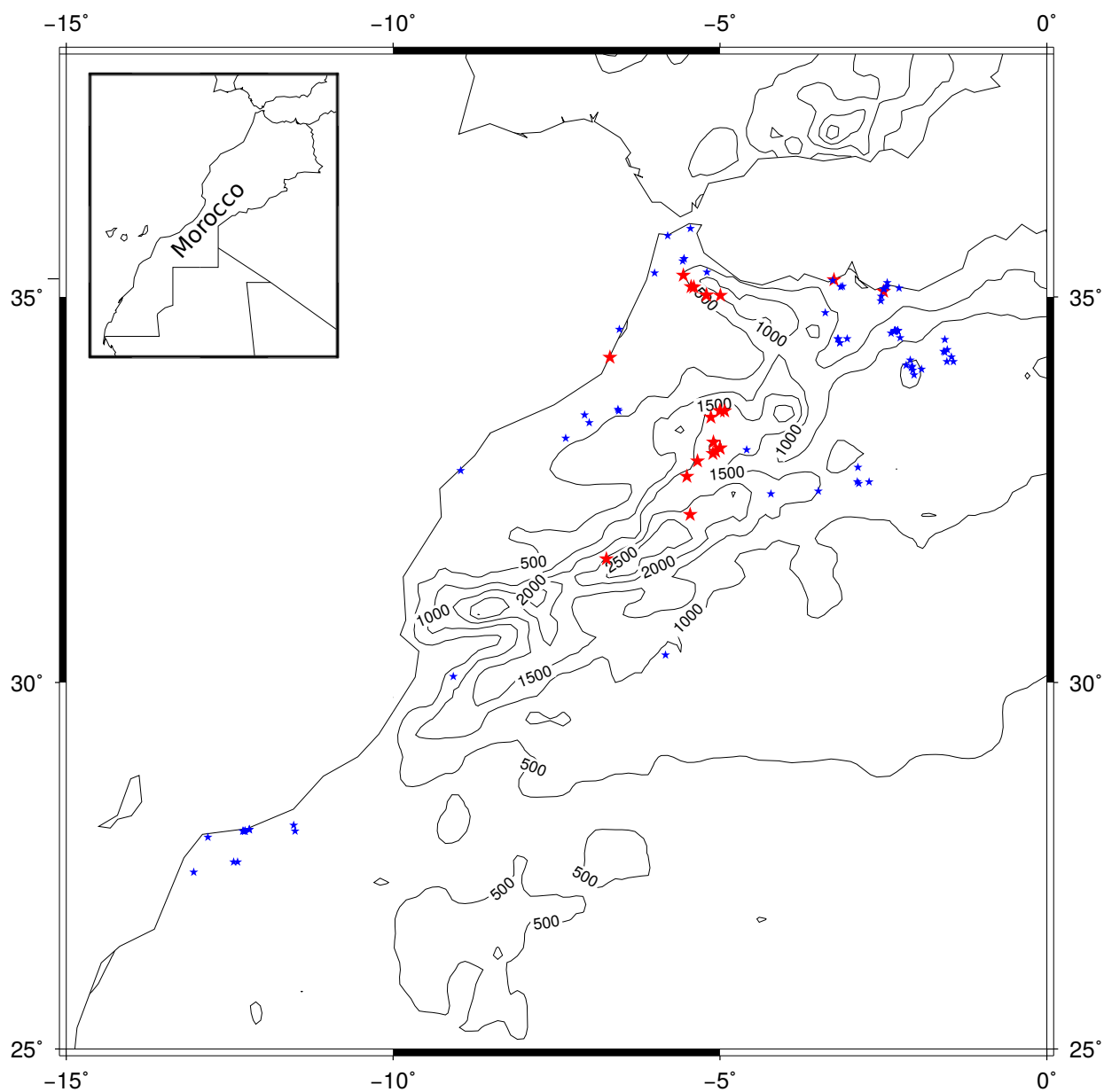
485 ***Acknowledgements***

486           This work stems from a workshop dedicated to the Leverhulme Trust-funded project  
487 'Changing the face of the Mediterranean: land cover and population since the advent of farming'  
488 organized in Mallorca in September 2017.

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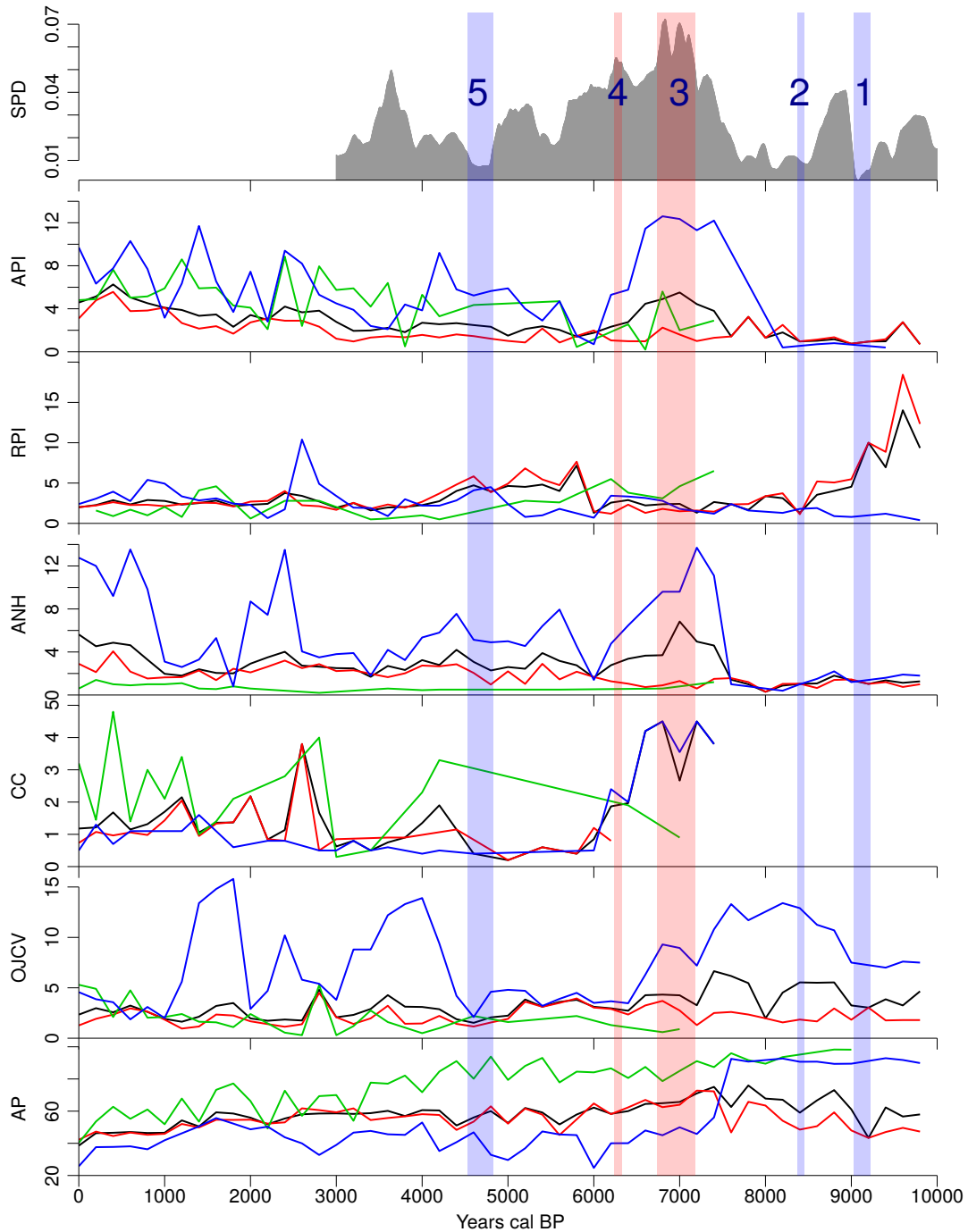
491 **Figure 1.** A. Location of the fossil pollen records (red stars) used for reconstructing  
492 anthropogenic markers, vegetation groups and pollen taxonomic richness. Pollen record  
493 numbers refer to table 1. B. Location of the archaeological sites (blue stars) from which we have  
494 obtained  $^{14}\text{C}$  measurements for evaluating past changes in human population in Morocco (SPD).  
495



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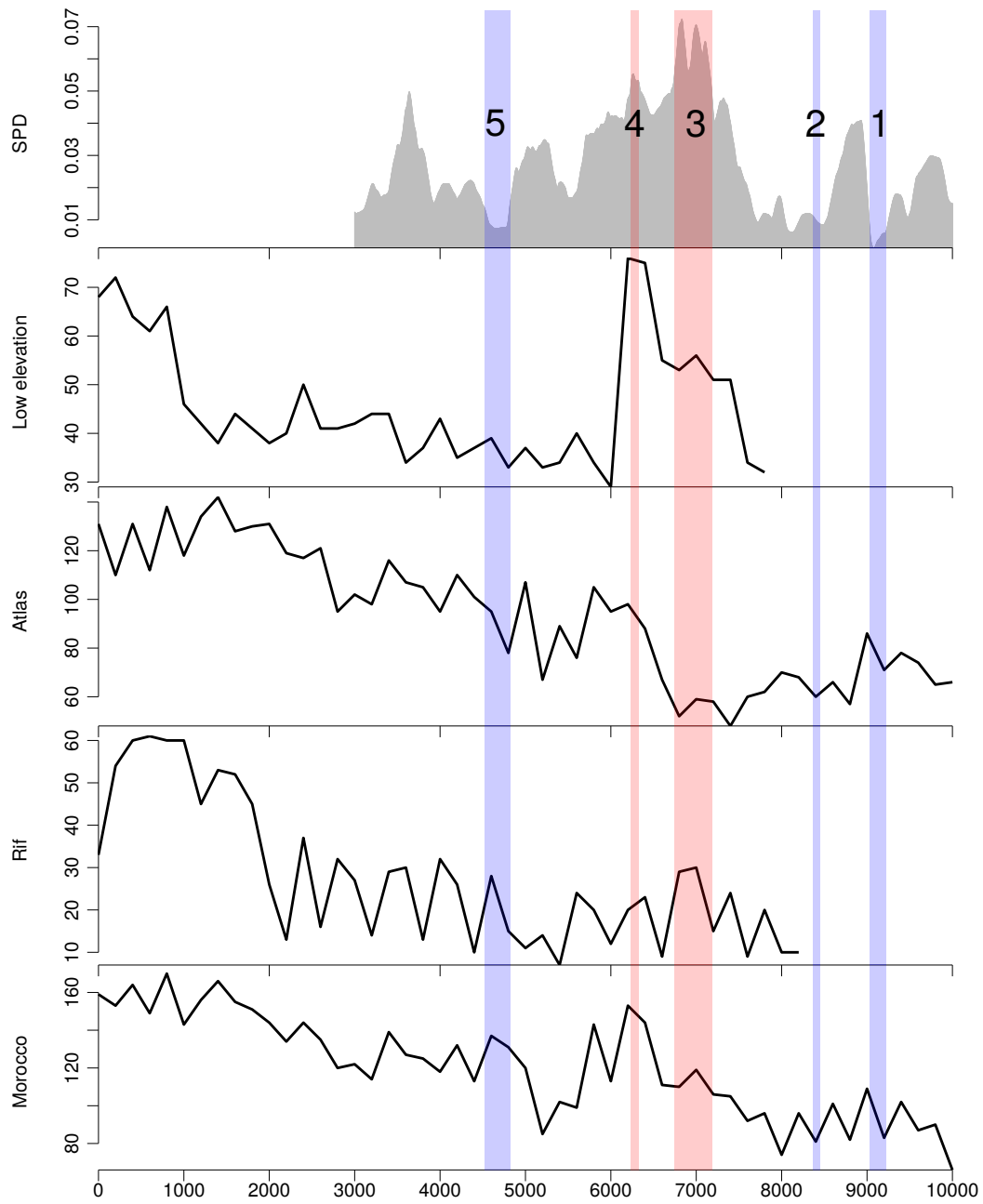


498 **Figure 2.** Percentages of anthropogenic pollen markers (API, RPI, ANH, CC and OJCV) and  
 499 arboreal pollen taxa (AP) during the Holocene in the Atlas mountains (red), the Rif  
 500 mountains (green), the lowlands (sites below 800m asl, blue) and Morocco (black, including  
 501 all pollen records). API = Anthropogenic Pollen index, RPI = Regional Pastoral indicators,  
 502 ANH = Anthropogenic nitrophilous herbs, CC= Cultures and crops and OJCV = *Olea-Juglans-*  
 503 *Castanea-Vitis*.  
 504



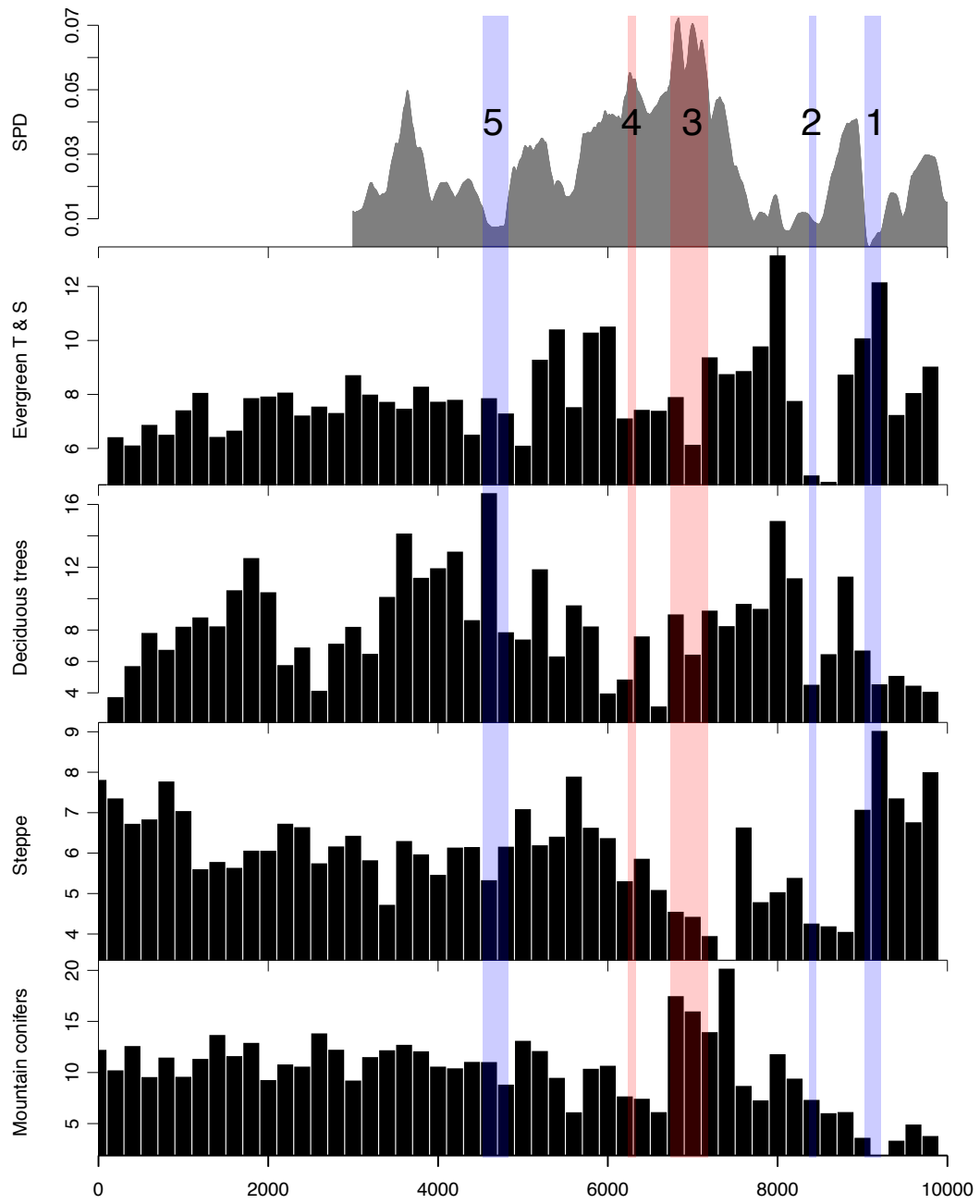
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507 **Figure 3.** Estimated pollen taxonomic richness using rarefaction analysis from the lowland  
508 sites (below 800m asl), the Rif and Atlas Mountains, and all datasets from Morocco.  
509



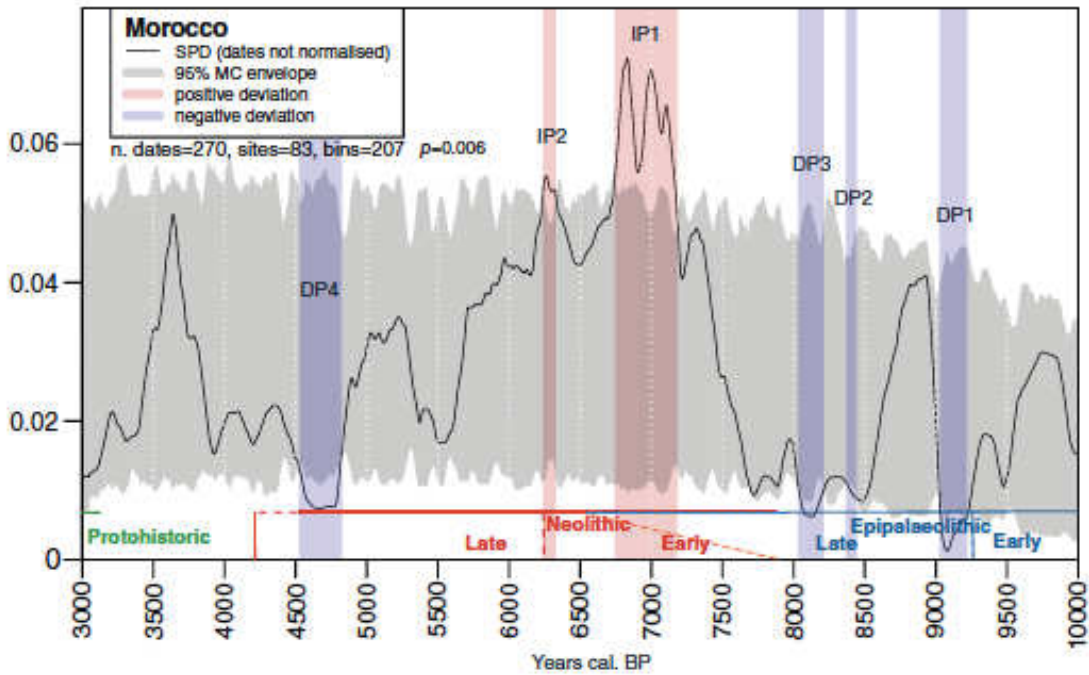
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512 **Figure 4.** Pollen percentages of four natural vegetation groups.  
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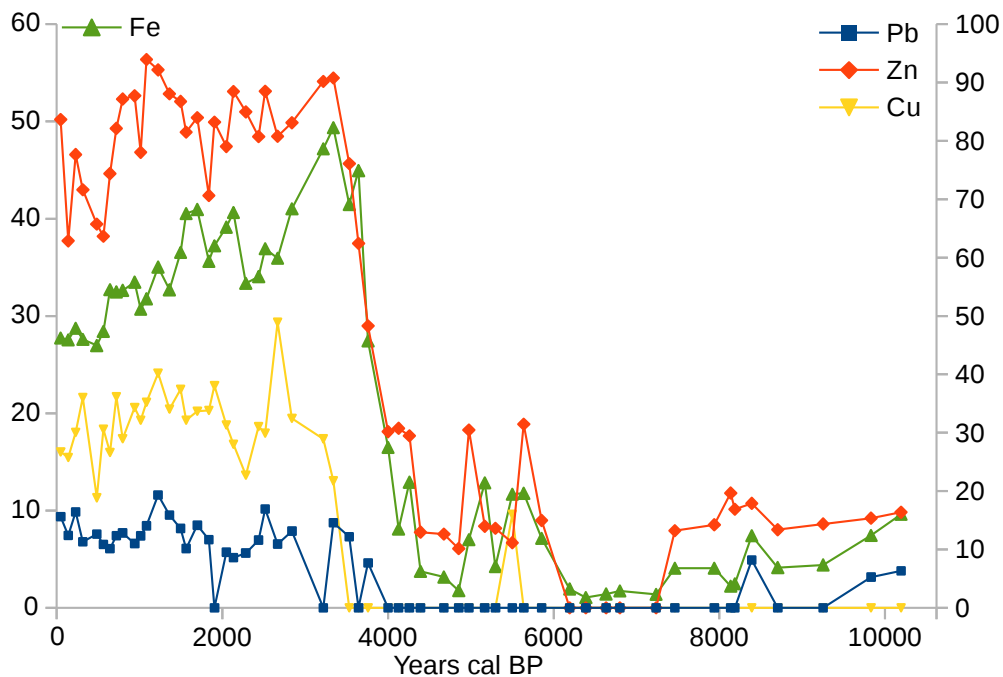


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516 **Figure 5.** Summed Probability Distribution (SPD) of unnormalised calibrated radiocarbon dates vs. a fitted logistic null model (95 % confidence grey envelope). Blue and red bands  
 517 indicate that chronological ranges within the observed SPD deviates negatively and  
 518 positively from the null model and corresponds to four significant decreases in human  
 519 population (events 1, 2, 3 and 6) and two significant increases (events 4 and 5). The  
 520 Epipalaeolithic and Neolithic periods have been defined according to Linstädter et al.  
 521 (2018) in Northern Morocco.  
 522



523 **Figure 6.** X-Ray measurements of Iron (Fe), Copper (Cu), Lead (Pb) and Zinc (Zn) in the Ait  
 524 Ichou fossil record collected in the Middle Atlas (Tabel et al., 2016)  
 525  
 526



527

528 **Table 1.** Pollen records used in the present study (displayed in figure 1A). All pollen records  
 529 from Reille (1976, 1977 and 1979) have been digitized from the original published pollen  
 530 diagrams and the raw data computed using the pollen sums.  
 531

| Site Name         | Location       | Elevation | Time span (approx) | Authors  |
|-------------------|----------------|-----------|--------------------|--|
| Aanasser          | Rif            | 1342      | 0-4000             | Reille, 1977, Cheddadi et al., 2015; 2017              |
| Abartete          | Rif            | 1260      | 0-8000             | Reille, 1976   |
| Bab El Karn       | Rif            | 1178      | 0-9000             | Cheddadi et al., 2016                                  |
| Col de Zad        | Middle Atlas   | 2138      | 0-3000             | Reille, 1976   |
| Hachlaf           | Middle Atlas   | 1700      | 0-6000; 0-16000    | Nourelbait et al., 2016; Tabel & Cheddadi, unpublished |
| Ifrah             | Middle Atlas   | 1610      | 4500-25000         | Cheddadi et al., 2009                                  |
| Ifri nEtsedda     | Rif            | 300       | 4500-10000         | Linstädter et al., 2016                                |
| Ifri Oudadane     | Rif            | 50        | 6000-10000         | Zapata et al., 2013                                    |
| Iguerda-Ait-Amama | Middle Atlas   | 2052      | 0-2500             | Reille, 1976   |
| Ishou             | Middle Atlas   | 1608      | 0-23000            | Tabel et al., 2016                                     |
| Marzine           | Rif            | 1400      | 0-2000             | Reille, 1976   |
| Mhad              | Rif            | 754       | 0-6000             | Cheddadi et al., 2015; 2017                            |
| Ras El Ma         | Middle Atlas   | 1633      | 0-18000            | Nourelbait et al., 2014                                |
| Sidi Ali          | Middle Atlas   | 2080      | 0-7500; 0-12000    | Lamb et al., 1999; Zielhofer et al., 2017              |
| Sidi bou Ghaba    | Rabat province | 20        | 0-6500             | Reille, 1979   |
| Tanakob           | Rif            | 726       | 0-1200             | Reille, 1976   |
| Tessaout          | High Atlas     | 2040      | 0-6000             | Reille, 1976   |
| Tifounassine      | Middle Atlas   | 1921      | 0-13000            | Tabel & Cheddadi, unpublished data                     |
| Tigalmamine       | Middle Atlas   | 1626      | 0-10000            | Lamb et al., 1995                                      |
| Tizi Ninouzane    | High Atlas     | 2591      | 0-2500             | Reille, 1976   |

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 533



534 **Table 2.** Taxa used to identify different human impacts within the Moroccan pollen records:  
 535 Anthropogenic Pollen index = API; Regional Pastoral indicators =RPI; Anthropogenic  
 536 nitrophilous herbs = ANH; Cultures and crops = CC; *Olea-Juglans-Castanea-Vitis* = OJCV.  
 537

| CC                    | API                                    | API                      |
|-----------------------|--|--------------------------|
| Cerealia-type         | Asteraceae subf. Cichorioideae         | Urtica                   |
| Cerealia              | Cannabaceae/Urticaceae                 | Urtica atrovirens        |
| Secale                | Centaurea                              | Urtica atrovirens-type   |
| Zea mays              | Centaurea cyanus                       | Urtica cf. U. dioica     |
|                       | Centaurea cyanus-type                  | Urtica cf. U. pilulifera |
| OJCV                  | Centaurea scabiosa                     | Urtica dioica            |
| Castanea sativa       | Centaurea scabiosa-type                | Urtica dioica-type       |
| Juglans               | Centaurea undiff.                      | Urtica dubia-type        |
| Juglans regia         | Cerealia                               | Urtica indeterminata     |
| Olea                  | Cerealia (excl. Secale)                | Urtica pilulifera        |
| Olea europaea         | Cerealia indeterminata                 | Urtica pilulifera-type   |
| Oleaceae              | Cerealia sp.                           | Urtica undiff.           |
| Vitis                 | Cerealia undiff.                       | Urtica unens             |
| Vitis vinifera        | Cerealia-type                          | Urtica-type              |
|                       | Cerealia-type (excl. Secale)           | Urtica/Humulus           |
| RPI                   | Cerealia-type cf. Avena/Triticum-group | Urtica/Parietaria        |
| Cirsium               | Cerealia-type cf. Hordeum-group        | Urticaceae               |
| Cirsium-type          | Cerealia-type undiff.                  | Urticaceae undiff.       |
| Galium                | Cerealia-type/Secale                   | Urticaceae/Moraceae      |
| Galium-type           | Cerealia-type/Triticum                 | Urticales                |
| Plantago lanceolata   | Cerealia-type/Triticum/Avena           |                          |
| Plantago pp.          | Cerealia-type/Zea                      |                          |
| Potentilla            | Cerealia/Avena-type                    |                          |
| Potentilla undiff.    | Cerealia/Hordeum-type                  |                          |
| Potentilla-type       | Cerealia/Secale                        |                          |
| Ranunculaceae         | Cerealia/Triticum-type                 |                          |
|                       | cf. Urtica                             |                          |
| ANH                   | Compositae subf. Cichorioideae         |                          |
| Anthemis-type         | Humulus/Cannabis/Urtica                |                          |
| Aster-type            | Plantago                               |                          |
| Boraginaceae          | Plantago cf. P. coronopus              |                          |
| Centaurea             | Plantago cf. P. lanceolata             |                          |
| Centaurea collina     | Plantago cf. P. major                  |                          |
| Centaurea cyanus      | Plantago cf. P. media                  |                          |
| Centaurea nigra-type  | Plantago coronopus                     |                          |
| Centranthus           | Plantago coronopus-type                |                          |
| Cirsium               | Plantago lanceolata                    |                          |
| Cirsium-type          | Plantago lanceolata-type               |                          |
| Convolvulaceae        | Plantago major                         |                          |
| Convolvulus           | Plantago major-type                    |                          |
| Dipsacaceae           | Plantago major/P. maritima             |                          |
| Echium                | Plantago major/P. media                |                          |
| Erodium-type          | Plantago major/P. media-type           |                          |
| Eryngium              | Plantago major/P. minor-type           |                          |
| Galium                | Plantago maritima                      |                          |
| Galium-type           | Plantago maritima-type                 |                          |
| Geraniaceae           | Plantago maritima/P. alpina            |                          |
| Geranium              | Plantago media                         |                          |
| Geranium-type         | Plantago media-type                    |                          |
| Hemlaria              | Plantago sp.                           |                          |
| Hemlaria-type         | Plantago undiff.                       |                          |
| Malva sylvestris-type | Plantago-type                          |                          |
| Malva-type            | Secale cereale                         |                          |
| Malvaceae             | Trifolium                              |                          |
| Portulaca oleracea    | Trifolium undiff.                      |                          |
| Solanum nigrum-type   | Trifolium-type                         |                          |

API = Anthropogenic Pollen Index; RPI = regional pastoral indicators; ANH = Anthropogenic nitrophilous herbs; CC = cultures and crops; OJCV: *Olea-Juglans-Castanea-Vitis*.

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540 **Table 3.** Pollen taxa grouped in the four natural vegetation groups

541

| Conifer trees          | Deciduous Trees                 | Steppe                         | Evergreen shrubs and trees     |
|------------------------|---------------------------------|--------------------------------|--------------------------------|
| Abies                  | Acer                            | Aster-type                     | Acacia                         |
| Cedrus                 | Alnus                           | Artemisia                      | Adenocarpus                    |
| Cupressaceae           | Carpinus                        | Asphodeline                    | Buxus                          |
| Juniperus              | Carpinus betulus-type           | Asphodelus                     | Ceratonia                      |
| Taxus baccata          | Castanea                        | Asteraceae subf. Asteroideae   | Ceratonia siliqua              |
| Tetraclinis articulata | Celtis                          | Asteraceae subf. Cichorioideae | Cistus ladanifer-type          |
|                        | Corylus                         | Centaurea                      | Cistaceae                      |
|                        | Fraxinus                        | Centaurea cyanus               | Coniferae (vesiculate)         |
|                        | Juglans                         | Centaurea cyanus-type          | Cupressus                      |
|                        | Ostrya                          | Centaurea nigra-type           | Cytisus-type                   |
|                        | Ostrya/Carpinus orientalis-type | Chenopodiaceae                 | Erica arborea-type             |
|                        | Populus                         | Compositae subf. Cichorioideae | Genista-type                   |
|                        | Prunus-type                     | Cyperaceae                     | Ilex                           |
|                        | Quercus canariensis             | Dipsacaceae                    | Laurus                         |
|                        | Quercus canariensis-type        | Dipsacus                       | Lavandula stoechas-type        |
|                        | Quercus cf. Q. canariensis      | Ephedra                        | Ligustrum                      |
|                        | Quercus faginea                 | Ephedra distachya              | Myrtaceae                      |
|                        | Quercus pyrenaica               | Ephedra distachya-type         | Myrtus communis                |
|                        | Quercus robur-type              | Ephedra fragilis               | Olea                           |
|                        | Salix                           | Ephedra fragilis-type          | Oleaceae                       |
|                        | Tilia                           | Poaceae                        | Phillyrea                      |
|                        | Ulmus                           | Sanguisorba minor              | Phillyrea latifolia            |
|                        |                                 | Scabiosa                       | Pinus                          |
|                        |                                 | Thymelaeaceae                  | Pinus halepensis               |
|                        |                                 |                                | Pinus halepensis/P. Pinea-type |
|                        |                                 |                                | Pinus pinaster                 |
|                        |                                 |                                | Pistacia                       |
|                        |                                 |                                | Quercus                        |
|                        |                                 |                                | Quercus coccifera              |
|                        |                                 |                                | Quercus ilex                   |
|                        |                                 |                                | Quercus ilex-type              |
|                        |                                 |                                | Quercus rotundifolia           |
|                        |                                 |                                | Quercus suber                  |
|                        |                                 |                                | Rhamnaceae                     |
|                        |                                 |                                | Rhamnus                        |
|                        |                                 |                                | Rhamnus alaternus-type         |
|                        |                                 |                                | Ribes                          |
|                        |                                 |                                | Ruscus                         |
|                        |                                 |                                | Tamarix                        |
|                        |                                 |                                | Viburnum                       |
|                        |                                 |                                | Vitis                          |
|                        |                                 |                                | Ziziphus                       |
|                        |                                 |                                | Ziziphus lotus                 |

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548 **Table 4.** Demographic peaks or troughs with statistically significant deviation from null model  
 549 (see Fig. 5). The dates summarise the duration of these events:

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| Event | Start (cal BP) | End (cal BP) | Duration (years) |
|-------|----------------|--------------|------------------|
| 1     | 9220           | 9030         | 190              |
| 2     | 8450           | 8370         | 80               |
| 3     | 8210           | 8030         | 180              |
| 4     | 7180           | 6740         | 440              |
| 5     | 6330           | 6240         | 90               |
| 6     | 4820           | 4530         | 290              |

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562 **Table 5.** Spearman's correlation coefficients between the pollen percentages of different  
 563 anthropogenic markers (ANH, API, CC, OJCV, RPI), vegetation groups and arboreal pollen (AP)  
 564 from fossil pollen records and archaeo-demographic datasets (SPD) by region and elevation  
 565 for the period 10000-3000 cal BP. Statistical significance: green:  $0.05 > P \text{ value} > 0.001$ ; red:  $P$   
 566 value  $< 0.001$

567

|                | Morocco     | Atlas      | Rif         | Low elevation |
|----------------|-------------|------------|-------------|---------------|
| AP             | 0,26        | 0,4        | 0,3         | -0,09         |
| ANH            | <b>0,63</b> | -0,12      | 0,22        | <b>0,59</b>   |
| API            | <b>0,61</b> | 0,05       | 0,13        | <b>0,61</b>   |
| CC             | <b>0,7</b>  | 0,16       | 0,03        | <b>0,74</b>   |
| OJCV           | 0,24        | <b>0,5</b> | 0,11        | 0,1           |
| RPI            | -0,17       | -0,23      | <b>0,61</b> | 0,06          |
| Taxa diversity | 0,26        | -0,19      | 0,31        | <b>0,51</b>   |
| Conifers       | 0,48        |            |             |               |
| Deciduous      | -0,16       |            |             |               |
| Evergreen      | -0,13       |            |             |               |
| Steppe         | -0,33       |            |             |               |

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## 570 **References**

- 571 Abel-Schaad D, Iriarte E, López-Sáez JA et al. (2018) Are *Cedrus Atlantica* forests in the Rif  
572 Mountains of Morocco heading towards local extinction? *The Holocene*, 28(6): 1023–1037
- 573 Arredi B, Poloni ES, Paracchini S et al. (2004) A predominantly neolithic origin for Y-  
574 chromosomal DNA variation in North Africa. *The American Journal of Human Genetics*  
575 75(2): 338-345.
- 576 Ballouche A and Marinval P (2003) Données palynologiques et carpologiques sur la  
577 domestication des plantes et l'agriculture dans le Néolithique ancien du Maroc  
578 septentrional. Le site de Kaf Taht el-Ghar. *Revue d'archéométrie* 27: 49-54.
- 579 Balsera V, Bernabeu Aubán J, Costa Caramé, M et al. (2015) The Radiocarbon Chronology of  
580 Southern Spain's Late Prehistory (5600–1000 Cal BC): a Comparative Review. Oxford.  
581 *Journal of Archaeology* 34(2): 139-156.
- 582 Behre KE (1981) The interpretation of anthropogenic indicators in pollen diagrams. *Pollen et*  
583 *Spores* 23(2): 225–245.
- 584 Bentayebi K, Abada F, Izhmad H et al. (2014) Genetic ancestry of a Moroccan population as  
585 inferred from autosomal STRs. *Meta Gene* 2: 427–38.
- 586 Bevan A and Crema ER (2018) rcarbon v1.2.0: Methods for calibrating and analysing  
587 radiocarbon dates. URL: <https://CRAN.R-project.org/package=rcarbon>
- 588 Bevan A, Colledge S, Fuller D et al. (2017) Holocene fluctuations in human population  
589 demonstrate repeated links to food production and climate. *Proceedings of the National*  
590 *Academy of Sciences* 201709190.
- 591 Birks HJB and Line JM (1992) The use of rarefaction analysis for estimating palynological  
592 richness from Quaternary pollen-analytical data. *The Holocene* 2(1): 1–10.
- 593 Bocquet-Appel J-P, Naji S, Linden MV, Kozłowski JK (2009) Detection of diffusion and contact  
594 zones of early farming in Europe from the space-time distribution of 14C dates. *Journal of*  
595 *Archaeological Science* 36: 807-820.
- 596 Bosch E, Calafell F, Perez-Lezaun A et al. (1997) Population history of North Africa: evi dence  
597 from classical genetic markers. *Human Biology* 69: 295–311.
- 598 Brakez Z, Bosch E, Izaabel H et al. (2001) Human mitochondrial DNA sequence variation in the  
599 Moroccan population of the Souss area. *Annals of human biology* 28(3): 295–307.
- 600 Brockerhoff EG, Jactel H, Parrotta JA et al. (2008) Plantation forests and biodiversity: Oxymoron  
601 or opportunity? *Biodiversity & Conservation* 17(5):925–51.
- 602 Campbell JFE, Fletcher WJ, Joannin S et al. (2017) Environmental drivers of Holocene forest  
603 development in the Middle Atlas, Morocco. *Frontiers in Ecology and Evolution* 5: 113.
- 604 Capuzzo G, Zanon M, Dal Corso M, Kirleis W and Barceló JA (2018) Highly diverse Bronze Age  
605 population dynamics in Central-Southern Europe and their response to regional climatic  
606 patterns. *PloS one* 13(8): p.e0200709.
- 607 Carrión JS, Fernández S, González-Sampériz P et al. (2010) Expected trends and surprises in the  
608 Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands.  
609 *Review of Palaeobotany and Palynology* 162(3): 458-475.
- 610 Cavalli-Sforza LL, Menozzi P and Piazza A (1993) Demic expansions and human evolution.  
611 *Science* 259(5095): 639-646.
- 612 Cheddadi R, Bouaissa O, Rhoujjati A et al. (2016) Environmental changes in the Moroccan  
613 western Rif mountains over the last 9,000 years. *Quaternaire* 27(1): 15-25.
- 614 Cheddadi R, Fady B, François L et al. (2009) Putative glacial refugia of *Cedrus atlantica* from  
615 Quaternary pollen records and modern genetic diversity. *Journal of Biogeography* 36:  
616 1361-1371.
- 617 Cheddadi R, Henrot AI, François L et al. (2017) Microrefugia, Climate Change, and Conservation  
618 of *Cedrus atlantica* in the Rif Mountains, Morocco. *Frontiers in Ecology and Evolution* 5:114.

- 619 Cheddadi R, Nourelbait M, Bouaissa O et al. (2015) A history of human impact on Moroccan  
620 mountain landscapes. *African Archaeological Review* 32(2): 233-248.
- 621 Cincotta RP, Wisnewski J and Engleman R. (2000) Human population in the biodiversity  
622 hotspots. *Nature* 404: 990-992.
- 623 Crema ER, Habu J, Kobayashi K et al. (2016) Summed Probability Distribution of 14C Dates  
624 Suggests Regional Divergences in the Population Dynamics of the Jomon Period in Eastern  
625 Japan. *PLoS One* 11(4):1-18.
- 626 Daugas JP, Raynal JP, El Idrissi A et al. (1998). Synthèse radiochronométrique concernant la  
627 séquence néolithique au Maroc. In Actes du colloque "14C et Archéologie": 349-353.
- 628 Desanges J (1981) The proto-Berbers J. *General history of Africa II*. 423-440.
- 629 El Baït MN, Rhoujjati A, Eynaud F et al. (2014) An 18 000-year pollen and sedimentary record  
630 from the cedar forests of the Middle Atlas, Morocco. *Journal of Quaternary Science* 29(5):  
631 423-432.
- 632 Fox JW (2013) The intermediate disturbance hypothesis should be abandoned. *Trends in  
633 ecology & evolution*, 28(2): 86-92.
- 634 Fyfe RM, Woodbridge J and Roberts CN (2018) Trajectories of change in Mediterranean  
635 Holocene vegetation through classification of pollen data. *Vegetation History and  
636 Archaeobotany*: 27: 351-364.
- 637 Gamble C, Davies W, Pettitt P et al. (2004) Climate change and evolving human diversity in  
638 Europe during the last glacial. *Philosophical Transactions of the Royal Society of London B:  
639 Biological Sciences* 359(1442): 243-254.
- 640 Görsdorf J and Eiwanger J (1999) Radiocarbon datings of late Palaeolithic, Epipalaeolithic and  
641 Neolithic sites in northeastern Morocco. *Mémoires de la Société préhistorique française* 26:  
642 365-369.
- 643 Hajar L, Haïdar-Boustani M, Khater C et al. (2010) Environmental changes in Lebanon during  
644 the Holocene: Man vs. climate impacts. *Journal of Arid Environments* 74(7): 746-755.
- 645 Hays JD, Imbrie J and Shackleton NJ (1976) Variations in the Earth's Orbit: Pacemaker of the Ice  
646 Ages. *Washington, DC: American Association for the Advancement of Science* 194(4270):  
647 1121-1132.
- 648 Hewitt GM (2000) The genetic legacy of the Quaternary ice ages. *Nature* 22, 405(6789): 907-  
649 13.
- 650 Hublin JJ, Ben-Ncer A, Bailey SE et al. (2017) New fossils from Jebel Irhoud, Morocco and the  
651 pan-African origin of Homo sapiens. *Nature* 546(7657): 289.
- 652 Hughes PD, Fenton CR and Gibbard PL (2011) Quaternary glaciations of the Atlas Mountains,  
653 North Africa. *Developments in Quaternary Sciences*. Elsevier 15: 1065-1074.
- 654 Hughes PD, Woodward JC and Gibbard PL (2006) Quaternary glacial history of the  
655 Mediterranean mountains. *Progress in physical geography* 30(3): 334-364.
- 656 Hughes PD, Fink D, Rodés Á et al. (2018) Timing of Pleistocene glaciations in the High Atlas,  
657 Morocco: New 10 Be and 36 Cl exposure ages. *Quaternary Science Reviews* 180: 193-213.
- 658 Ibouhouten H, Zielhofer C, Mahjoubi R et al. (2010) Archives alluviales holocènes et occupation  
659 humaine en Basse Moulouya (Maroc nord oriental). *Géomorphologie: Relief, Processus,  
660 Environnement* 16 (1): 41-56.
- 661 IUCN (2018) The IUCN Red List of Threatened Species. Version 2018-1.
- 662 Jalut G, Dedoubat JJ, Fontugne M et al. (2009) Holocene circum-Mediterranean vegetation  
663 changes: climate forcing and human impact. *Quaternary international* 200(1-2): 4-18.
- 664 Kaplan JO, Krumhardt KM and Zimmermann N (2009) The prehistoric and preindustrial  
665 deforestation of Europe. *Quaternary Science Reviews* 28: 3016-3034.
- 666 Lamb HF, Damblon F and Maxted RW (1991) Human impact on the vegetation of the Middle  
667 Atlas, Morocco, during the last 5000 years. *Journal of Biogeography* 18: 519-532.



- 668 Lavorel S. Ecological diversity and resilience of Mediterranean vegetation to disturbance.  
669 *Diversity and Distributions* 1999;5:3–13.
- 670 Leydet, M. (2007–2018). The European pollen database. [http://www.eu](http://www.europepollendatabase.net/)  
671 [ropeanpollendatabase.net/](http://www.europepollendatabase.net/)
- 672 Linstädter J, Aschrafi M, Ibouhouten H et al (2012) Flussarchäologie der Moulouya-  
673 Hochflutebene, NO-Marokko. *Madriider Mitteilungen* 53: 1-84.
- 674 Linstädter J, Broich M and Weninger B (2018) Defining the Early Neolithic of the Eastern Rif,  
675 Morocco - Spatial distribution, chronological framework and impact of environmental  
676 changes. *Quaternary International* 472: 272-282.
- 677 Linstädter J, Kehl M, Broich M et al. (2016) Chronostratigraphy, site formation processes and  
678 pollen record of Ifri n'Etsedda, NE Morocco. *Quaternary International* 410: 6-29.
- 679 López-Sáez JA and López-Merino L (2008) Antropización y neolitización durante el Holoceno  
680 en Marruecos: Una aproximación paleopalinológica. In *Act. IV Congreso del Neolítico*  
681 *Peninsular I. Museo Arqueol Alicante, Alicante* 438-444.
- 682 López-Sáez JA, Abel D, Bokbot Y et al (2013) Paisajes neolíticos del noroeste de Marruecos:  
683 Análisis arqueopalinológico de la Cueva de Boussaria. In: Goncalves VS, Diniz M and Sousa  
684 AC (eds) 5° Congresso do Neolítico Peninsular. Lisboa: Universidade de Lisboa, pp. 92–97.
- 685 Lotter AF (1998) Late-glacial and Holocene vegetation history and dynamics as shown by  
686 pollen and plant macrofossil analyses in annually laminated sediments from Soppensee,  
687 central Switzerland. *Vegetation History and Archaeobotany* 8(3): 165-184.
- 688 Manning K, Timpson A, Colledge S et al. (2014) The chronology of culture: a comparative  
689 assessment of European Neolithic dating approaches. *Antiquity* 88(342): 1065-1080.
- 690 Mercuri AM (2008) Human influence, plant landscape evolution and climate inferences from  
691 the archaeobotanical records of the Wadi Teshuinat area (Libyan Sahara). *Journal of Arid*  
692 *Environments* 72(10): 1950–1967.
- 693 Mercuri AM and Sadori L (2012) Climate changes and human settlements since the Bronze age  
694 period in central Italy. *Rendiconti Online della Società Geologica Italiana* 18: 32–34.
- 695 Mercuri AM, Mazzanti MB, Florenzano A et al (2013a) Anthropogenic pollen indicators (API)  
696 from archaeological sites as local evidence of human-induced environments in the Italian  
697 Peninsula. *Annali Di Botanica* 3: 143-153.
- 698 Mercuri AM, Mazzanti MB, Florenzano A et al (2013b) *Olea, Juglans* and *Castanea*: The OJC group  
699 as pollen evidence of the development of human-induced environments in the Italian  
700 peninsula. *Quaternary International* 303: 24-42.
- 701 Mercuri AM, Sadori L and Uzquiano OP (2011) Mediterranean and North-African cultural  
702 adaptations to mid-Holocene environmental and climatic changes. *The Holocene* 21(1):  
703 189-206.
- 704 Michczyńska DJ and Pazdur A (2004) Shape analysis of cumulative probability density function  
705 of radiocarbon dates set in the study of climate change in late glacial and holocene.  
706 *Radiocarbon* 46 (2): 733-744.
- 707 Michczyńska DJ, Michczyński A, Pazdur A (2007) Frequency distribution of radiocarbon dates  
708 as a tool for reconstructing environmental changes. *Radiocarbon* 49 (2): 799-806.
- 709 Mikdad A, Eiwanger J, Atki H et al. (2000) Recherches préhistoriques et protohistoriques dans  
710 le Rif oriental (Maroc): rapport préliminaire. *Beiträge zur Allgemeinen und Vergleichenden*  
711 *Archäologie* 20: 109-167.
- 712 Mikdad A, Nekkal F, Nami M et al. (2012) Recherches sur le peuplement humain et l'évolution  
713 paléoenvironnementale durant le Pléistocène et l'Holocène au Moyen Atlas central:  
714 résultats préliminaires. *Bulletin d'Archéologie Marocaine* 22: 53-71.
- 715 Morales J, Pérez-Jordà G, Peña-Chocarro L et al. (2013) The origins of agriculture in North-West  
716 Africa: macro-botanical remains from Epipalaeolithic and Early Neolithic levels of Ifri

- 717 Oudadane (Morocco). *Journal of Archaeological Science* 40(6): 2659-2669.
- 718 Myers N, Mittermeier RA, Mittermeier CG et al. (2000) Biodiversity hotspots for conservation  
719 priorities. *Nature* 403(6772): 853.
- 720 Palmisano A, Bevan A and Shennan S (2017) Comparing archaeological proxies for long-term  
721 population patterns: An example from central Italy. *Journal of Archaeological Science* 87:  
722 59-72.
- 723 Palmisano A, Woodbridge J, Roberts N et al. (2019, in press) Holocene Landscape Dynamics and  
724 Long-term Population Trends in the southern Levant. *The Holocene*.
- 725 Pausas JG, Llovet J, Anselm R, Vallejo R (2008) Are wildfires a disaster in the Mediterranean  
726 basin? A review Vegetation changes Shrublands dominated by resprouting species.  
727 *International Journal of Wildland Fire* 17:1-22.
- 728 Pearson RG, Dawson TP 2003. Predicting the impacts of climate change on the distribution of  
729 species: are bioclimate envelope models useful? *Global Ecology & Biogeography* 12(5):  
730 361-71.
- 731 Quézel P and Médail F (2003) Ecologie et biogéographie des forêts du bassin méditerranéen.  
732 *Paris : Elsevier* 572.
- 733 Rando JC, Pinto F, González AM et al. (1998) Mitochondrial DNA analysis of Northwest African  
734 populations reveals genetic exchanges with European, Near Eastern, and sub Saharan  
735 populations. *Annals of human genetics* 62(6): 531-50.
- 736 Rankou H, Culham A, Jury SL et al. (2013) The endemic flora of Morocco. *Phytotaxa*, 78(1): 1-  
737 69.
- 738 Reille M (1976) Analyse pollinique de sédiments postglaciaires dans le Moyen Atlas et le Haut  
739 Atlas marocains : premiers résultats. *Ecologia Mediterranea* 2: 155-170.
- 740 Reille M (1977) Contribution pollenanalytique a l'histoire holocène de la végétation des  
741 montagnes du rif (Maroc septentrional). *Recherches françaises sur le Quaternaire INQUA*  
742 50: 53-76.
- 743 Reille M (1979) Analyse pollinique du lac de Sidi Bou Rhaba, littoral atlantique (Maroc).  
744 *Ecologia Mediterranea* 4: 61-65.
- 745 Reimer PJ, Bard E, Bayliss A et al. (2013) IntCal13 and Marine13 radiocarbon age calibration  
746 curves 0-50,000 Years cal BP. *Radiocarbon* 55(4): 1869-1887.
- 747 Rick JW (1987) Dates as Data: An examination of the Peruvian radiocarbon record. *American*  
748 *Anitquity* 52: 55-73.
- 749 Roberts N, Woodbridge J, Bevan A et al. (2018) Human responses and non-responses to climatic  
750 variations during the last glacial-interglacial transition in the eastern Mediterranean.  
751 *Quaternary Science Reviews* 184: 47-67.
- 752 Saadi F and Bernard J (1991) Rapport entre la pluie pollinique actuelle, le climat et la végétation  
753 dans les steppes à *Artemisia* et les milieux limitrophes au Maroc. *Palaeoecology of Africa*  
754 *and the Surrounding Islands* 22: 67-86.
- 755 Sadori L, Jahns S and Peyron O (2011) Mid-Holocene vegetation history of the central  
756 Mediterranean. *The Holocene* 21(1): 117-129.
- 757 Shennan, S. 2018 *The first farmers of Europe. An evolutionary perspective*. Cambridge UP.
- 758 Shennan S, Edinborough K (2007) Prehistoric population history: from the late Glacial to the  
759 late Neolithic in Central and Northern Europe. *Journal of Archaeological Science* 34: 1339-  
760 1345.
- 761 Shennan S, Downey SS, Timpson A et al. (2013) Regional population collapse followed initial  
762 agriculture booms in mid-Holocene Europe. *Nature Communications* 4: 2486.
- 763 Tabel J, Khater C, Rhoujjati A et al. (2016) Environmental changes over the past 25 000 years in  
764 the southern Middle Atlas, Morocco. *Journal of Quaternary Science* 31(2): 93-102.
- 765 Thuiller W, Richardson DM, Pysek P et al. (2005) Niche-based modelling as a tool for predicting

766 the risk of alien plant invasions at a global scale. *Global Change Biology* 11: 2234–50.

767 Timpson A, Colledge S, Crema E et al. (2014) Reconstructing regional population fluctuations  
768 in the European Neolithic using radiocarbon dates: a new case-study using an improved  
769 method. *Journal of Archaeological Science* 52: 549-557.

770 Turchin, P. 2001. Does population ecology have general laws? *Oikos* 94 (1), 17-26.

771 Van Der Plicht J, Bruins HJ and Nijboer AJ (2009) The Iron Age around the Mediterranean: a  
772 High Chronology perspective from the Groningen radiocarbon database. *Radiocarbon*,  
773 51(1), 213-242.

774 van de Loosdrecht M, Bouzouggar A, Humphrey L et al (2018) Pleistocene North African  
775 genomes link Near Eastern and sub-Saharan African human populations. *Science*  
776 360(6388), 548-552.

777 Vitousek PM, Mooney HA, Lubchenco J et al. (1997) Human domination of Earth's ecosystems.  
778 *Science* 277(5325): 494-499.

779 Weninger B, Clare L, Jöris O et al. (2015) Quantum theory of radiocarbon calibration. *World*  
780 *Archaeology* 47(4): 543-566.

781 Weninger B, Clare L, Rohling E et al. (2009) The Impact of Rapid Climate Change on Prehistoric  
782 Societies during the Holocene in the Eastern Mediterranean. *Documenta Praehistorica*  
783 *Ljubljana* 36: 7-59.

784 Williams AN (2012) The use of summed radiocarbon probability distributions in archaeology:  
785 a review of methods. *Journal of Archaeological Science* 39(3): 578–589.

786 Woodbridge J, Roberts CN and Fyfe RM (2018) Holocene vegetation and land-cover dynamics  
787 in the Mediterranean from pollen data. *Journal of Biogeography* 45: 2159-2174.

788 Zapata L, López-Sáez JA, Ruiz-Alonso M (2013) Holocene environmental change and human  
789 impact in NE Morocco: Palaeobotanical evidence from Ifri Oudadane. *The Holocene* 23(9):  
790 1286-1296.

791 Zielhofer C, Faust D, Linstädter J (2008) Late Pleistocene and Holocene fluvial records in the  
792 Western Mediterranean: hydroclimatical changes and past human response. *Quaternary*  
793 *International* 181: 39-54.

794 Zielhofer C, Fletcher WJ, Mischke S et al. (2017) Atlantic forcing of Western Mediterranean  
795 winter rain minima during the last 12,000 years. *Quaternary Science Reviews* 157: 29-51.

796